

Predictability, contingency, and convergence in late succession: Slow systems and complex data-sets

Woods, Kerry D.

Natural Sciences, Bennington College, Bennington VT 05201, USA; E-mail kwoods@bennington.edu

Abstract

Questions: Are community dynamics in old-growth forests predictable? Convergent? Equilibrial? Are answers to these questions dependent on temporal and spatial scale? How can complex, long-term observational data be used most powerfully to address these questions?

Location: 100-ha tract of old-growth cool-temperate forest in northern Michigan, USA.

Methods: Woody stems were measured, on 243 permanent plots, several times, at varying intervals and intensity, over 70 years. A range of visualization tools and multivariate statistics were used to extract patterns and address questions posed.

Results: This ancient forest is not equilibrial; compositional trends suggest that changes are competitively driven and reflect long-lasting effects of disturbance. Predictability of community change varies across environmental gradients, with interval between samples, with spatial scale, and depending on type of predictability being assessed. Plot trajectories in species-space and changes in diversity suggest successional convergence within some habitats, but not across habitats. Dynamics are strongly structured at the scale of 'habitat-patches'.

Conclusions: Appropriate address of questions about community dynamics requires observational data of appropriate spatial and temporal scale and resolution. Powerful use of such data-sets calls for data-management and analysis tools that are robust with respect to irregularities in design and data structure. While interpretation of long-term descriptive data is challenging, appropriate analyses cast light on late successional dynamics, allowing address of models and hypotheses that are otherwise difficult to test.

Keywords: *Acer saccharum*; *Betula alleghaniensis*; Ecoinformatics; *Fagus grandifolia*; Hemlock-northern hardwood forest; Old-growth forest; Permanent plot; *Thuja occidentalis*; *Tsuga canadensis*.

Nomenclature: Gleason & Cronquist (1991).

Abbreviation: RNA = Dukes Research Natural Area.

Introduction

Despite a long history of debate about dynamics of late-successional forests (Are they stable? Equilibrial? Structured by ecological interactions? 'Neutrally' assembled?), opportunities for rigorous testing of competing hypotheses are rare. Studies employing space-for-time substitutions (for example, chronosequences and extrapolations from spatial pattern of canopy gaps and regeneration) are frequent, but involve risky assumptions about history (Pickett 1989). Paleoecology offers long-term perspective, but only rarely provides spatial and temporal resolution requisite for understanding stand-scale dynamics (but see Arseneault 2004; Parshall 1995). Dendrochronology and stand reconstruction can provide great detail and resolution at the scale of centuries (e.g. Henry & Swan 1974; Abrams et al. 1998) but are extremely labor-intensive. Simulation models can provide both long-term perspectives and high resolution (see Busing & Maily 2004), but require empirical data for assessment of accuracy.

While combinations of such approaches can be powerful (e.g. Bakker et al. 1996; Baker et al. 2002), they all, ultimately, involve assumptions that can be most rigorously tested only with longitudinal data. Planned longitudinal studies of slow, late-successional communities, however, are logistically prohibitive. Consequently, strong empirical evidence concerning dynamic properties of communities is generally from constructed or early-successional communities of short-lived species. Quantitative, plot-based studies of temperate forest vegetation spanning more than a decade are rare (Woods 2000a, b), and even fewer concern late-successional stands (but see Franklin & DeBell 1988; Harcombe et al. 2002). Thus, current understanding of such vegetation retains a large anecdotal element.

This situation places a high premium on exploitation of historical data sets, especially those from permanent plots (Bakker et al. 1996). However, powerful use of historical data can be constrained by special problems of information management and analysis. Initial measurements in historical data-sets are likely to have been structured for purposes other than assessment of

long-term community dynamics. Measurement techniques, precision, and intervals may have varied across measurements, or data preservation may be incomplete. Adopters of historical data-sets must address all of these constraints in analysis and interpretation.

Here, I use spatially intensive, multi-temporal data from a diverse old-growth forest landscape in Michigan, USA both to address some current questions about behavior of old-growth systems and to explore tools for extracting information from complex data-sets. Ecological questions include:

1. How stable are these forests at scales of decades and longer? Are they better described by equilibrium or non-equilibrium models?

2. Are changes predictable from current composition or site characteristics, or is knowledge of site history necessary?

3. Does composition tend to converge or diverge?

4. Do answers to these questions vary with temporal or spatial scale?

Traditional succession-to-climax theory suggests that, with time, the signature of stand history becomes less visible in stand properties, dynamics become slower and more predictable from current composition (Christensen & Peet 1984), and community properties converge within habitats (but see Lepš & Rejmánek 1991). Non-equilibrium community models challenge these predictions (Chesson & Chase 1986) and suggest that explanation and prediction of community properties may require reference to particularities of history; more recent 'neutral' models may imply that dynamics of late-successional forests are predictable only in broad statistical terms if at all.

Study site and prior results

Study site. The 100-ha Dukes Research Natural Area (RNA) is part of the Hiawatha National Forest in northern Michigan, USA (46°02' N 87°09' W). A cool-temperate, continental climate is tempered by Lake Superior, 14 km to the N. Average annual temperature, 1970-2000, at Marquette, MI (ca. 30 km NW) is 4.2 °C (January average = -10.9 °C, July average = 18.3 °C), total annual precipitation averages 925 mm with nearly half as snowfall (cumulative annual snowfall averages > 4000 mm). Elevation is ca. 330 m, about 100 m above Lake Superior. Upland soils are developed in thick glacial till over Paleozoic sedimentary deposits.

Regionally, late-successional, mesic forests are described as 'hemlock-northern hardwood'. There is no record or evidence of logging within the RNA. Increment cores confirm mixed-age status, with maximum ages for dominant species approaching 400 year (unpubl.

data), indicating a lack of stand-initiating disturbance for several centuries. The RNA is buffered on all sides by never-cleared stands managed with long cutting cycles and high residual basal area.

Although total relief within the RNA is < 10 m, soil drainage, texture, and chemistry vary greatly. Peaty wetlands are dominated by *Thuja occidentalis*, *Picea mariana*, *Fraxinus nigra*, *Acer rubrum*, and, formerly, *Ulmus americana*. Uplands (sandy and silty loams of varying chemistry) are dominated by *Acer saccharum*, *Fagus grandifolia*, *Tsuga canadensis*, *Betula alleghaniensis*, and *Acer rubrum*. *Fagus* has been present locally < 1000 year (Woods & Davis 1989), and its western range-limit is < 10 km from the RNA.

Data-set. In 1935, 246 circular plots of 0.2 acre (= 809 m²) were established on a 2 × 5 chain (ca. 40 × 100 m) grid over the RNA, each marked with an iron pipe at center. All stems > 5 in (12.7 cm) DBH were recorded by diameter and species for 238 plots. In 1948, 123 plots (alternating along grid-lines) were measured using the same protocol. Between 1974 and 1980, 243 plots were measured with stems tallied to minimum dbh of 0.5 in (1.3 cm). From 1989 to 1992, for 122 upland plots all woody stems > 5 cm DBH were recorded with stems > 2 cm DBH subsampled, and all measured stems were mapped; these plots have been remeasured every five years subsequently. From 1999-2004 an additional 75 peaty wetland forest plots were similarly remeasured without stem-mapping. During the 1990s soil samples from upland plots were analysed for acidity and principal mineral nutrients. See Woods (2000b, 2004) for further detail.

Prior analyses. Compositional changes in upland stands from 1935 to 1989-1992 (Woods 2000b) suggest competitively driven, successional dynamics. Populations of shade-tolerant species, particularly *Fagus grandifolia*, expanded, while less tolerant species, particularly *Betula alleghaniensis* declined, suggesting competitive sorting trending toward dominance by the most shade-tolerant species. Patterns in upland stands were related to substrate properties (Woods 2000b). *Acer saccharum* was dominant on sites with higher cation concentrations and pH; *Tsuga* dominance was associated with deep mor humus and low pH; *Fagus* populations were densest and increased most in areas with well-developed shallow hard-pan, where canopy diversity was also highest.

Woods (2000b) interprets these patterns as most consistent with a non-equilibrium dynamic where historical events – disturbances or environmental changes – have prevented displacement of less competitive species. Immediate consequences of a major wind-disturbance in 2002, based on a partial resampling of upland plots,

were consistent with this model (Woods 2004). Canopy destruction (to 30% of basal area locally) was patchy, with gaps averaging about 800-1000 m², potentially favoring regeneration of less tolerant species that had declined since 1935. Disturbance intensity was greatest in areas with well-developed hard-pan, and mortality risk varied with species; shade-tolerant hardwoods *Fagus* and *Acer* suffered disproportionately high mortality.

New analyses: Methods

Analyses here incorporate some previously missing data and remeasurements of upland stands through 2004, extending earlier analyses (Woods 2000b) by a decade. Plots from peaty wetlands are included, extending analyses over broader ecological gradients. New analyses are developed to address questions about community dynamics and scale.

General patterns. I assigned measurements to several 'sampling periods'. For all plots, the first three periods are 1935, 1948, and 1974-1980. For upland forests, recent measurements were assigned to three sampling periods; 1989-1992; 1997-1999 ('pre-storm'); and 2002-2004 ('post-storm'). For wetland forests, all recent measurements (1999-2004) were treated as a single sampling period (storm damage was not as great in lower-lying, lower-stature wetland forests, and most wetland plots have been sampled only once since 1999). Comparisons, therefore, address intervals ranging from five years to nearly seven decades. Sample sizes vary widely among comparisons. All analyses reported here include only stems > 12.6 cm DBH for consistency with earliest measurements.

Published analyses showed a strong, habitat-related spatial pattern across the stand (Woods 2000b, 2004). I used non-metric multidimensional scaling (NMS) ordinations (PC-Ord, McCune & Mefford 1999) for individual and multiple dates to visualize overall compositional pattern. Cluster analysis (PC-Ord, Sørensen distance, Ward's linkage method), and maps of species abundances and soil properties (Woods 2000b) were used to assign plots to spatially coherent and compositionally similar groups associated with substrate properties; these groups are subsequently referred to as 'habitat-patches' or simply 'patches'. Thus, dynamics can be assessed at three spatial scales: the full stand; the 'habitat-patch' scale; and the single-plot scale.

Predictability. Predictability of stand dynamics may be qualitatively assessed by visual inspection of change vectors in multi-temporal ordinations; a highly ordered vector field (Fulton & Harcombe 2002), with local

coherence of vector direction and length, suggests that dynamics may be predictable from initial composition. A more chaotic vector field suggests unpredictability.

Mantel tests (procedures as in McCune & Grace 2002), which assess correspondences between distance matrices, were used for more quantitative assessment of predictability. Two types of tests were employed for a variety of plot groups and sample intervals. 'Composition predictability' is taken as predictability of end-composition given initial composition and is assessed by the correspondence between distance matrices derived from the initial composition matrix and the final composition matrix. I define 'trajectory predictability' as predictability of change-vectors given initial composition. It is measured as the correspondence between the distance matrix derived from an initial composition matrix and the distance matrix derived from the 'change matrix' produced by subtracting the initial composition matrix from the final composition matrix.

Different assumptions about community dynamics predict different patterns and relationships between these two properties. For example, in near-equilibrium stands, composition should change little from initial composition (high composition predictability), but trajectories of compositional change may be essentially random fluctuations at plot-scale (low trajectory predictability). Due to multiple testing and because sample sets are not independent, significance values for Mantel results are suspect, but patterns with respect to time-scale and sample period of habitat-patch and composition may be informative. For all Mantel tests, Euclidean distance and Mantel's asymptotic approximation method (McCune & Grace 2002) were used.

Effects of spatial scale

To assess whether habitat-patches exhibited dynamics distinct from other patches of similar or different composition, or from the stand as a whole, multiple-range permutation procedures (MRPP) were applied to change matrices over various measurement intervals. MRPP provide a non-parametric test for differences between groups of entities (McCune & Grace 2002) – in this instance, differences between groups of plot change vectors in species-space. MRPP was used to assess whether (1) trajectories in species-space for plots in different habitat-patches were predictably different (independent of origin), and (2) whether plots in spatially separated, but compositionally similar habitat-patches exhibited similar trajectories.

Convergence. To assess convergence of compositional trajectories for selected intervals and habitat-types, I compared distributions of plot-plot distances in species-

space between sample periods for various combinations of habitat patches. Convergence should be manifest as increasing clustering of plots in species-space over time. If plots converge generally towards a particular composition, the distribution of plot-plot distances should become narrower around a smaller median value. If convergence is towards multiple loci in species-space (e.g. if competitive dominance shifts along sampled gradients), distances will decrease within clusters of plots converging towards the same composition, but increase for pairs of plots moving towards different loci, and the overall distribution of plot-plot distances should become more dispersed and, eventually, polymodal. Differences between distance distributions were assessed with the

non-parametric Kolmogorov-Smirnov test.

If convergence is due to competitive replacement, diversity should decrease. Changes in diversity indices between the 1935, 1970s and recent pre-storm sample intervals were assessed using repeated measures ANOVAs, including models nesting plots within patches and habitat-types; *t*-tests were used for specific comparisons of diversity values for plots for particular dates and patches or habitat-types. Two diversity indices were used: Shannon's $H = -\sum p_i \ln(p_i)$, where p_i is basal area relativized within plot and summation is over all species in plot; and evenness expressed as $J = H/\ln(S)$, where S = total number of species.

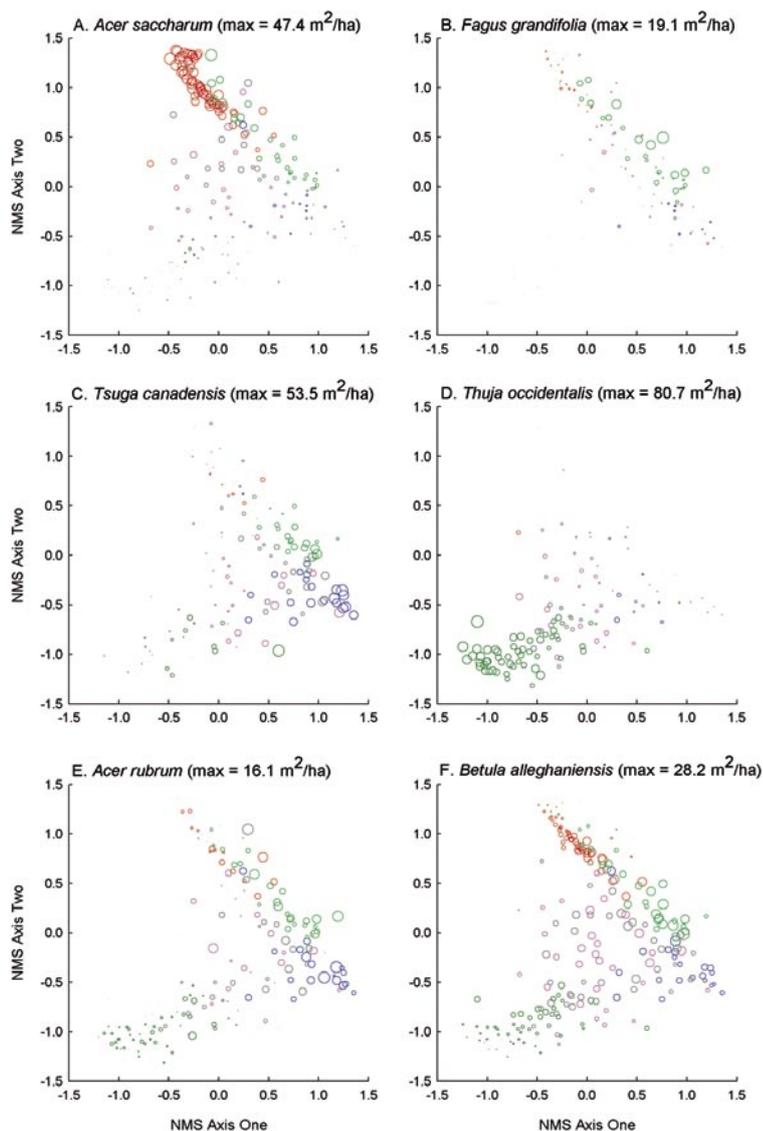


Fig. 1. Distribution of major species in two-dimensional non-metric multi-dimensional scaling ordination of 1974-1980 sampling (Sørensen distance, procedure as recommended by McCune & Grace 2002:131-136. 40 runs of real data yielded recommended data reduction of 2 axes, final stress = 12.5 after 100 iterations; Monte Carlo tests with 100 runs randomized data indicate both axes significant ($p = -0.02$), cumulative $r^2 = 0.64$). Symbol area proportional to plot basal area, scaled to species maximum. Symbol color corresponds to habitat-type (Fig. 2); gray symbols are plots not sampled after 1980, or not assigned to groups.

Results

Compositional patterns and spatial scale. Ordinations of all plots, expanded patterns described in Woods (2000b) to include swamp forests. Ordinations showed continuous compositional variation (Fig. 1) with strong separation of shade-tolerant canopy dominants (*Acer saccharum*, *Fagus*, *Tsuga*, and *Thuja*). Distributions of less-tolerant canopy species (*Acer rubrum* and *Betula alleghaniensis*) in the ordination were generally broader. *Thuja* dominance is concordant with peaty wetlands (not included in Woods 2000b) where *Picea mariana*, *P. glauca*, and *Fraxinus nigra* also display occasional high basal areas.

While compositional gradients are continuous in species-space, habitat is patchy, creating areas of relatively homogeneous composition. Cluster analysis (of the most complete 1974-1980 sample), in combination with ordinations and distributions of species and soil properties (Woods 2000b) allowed definition of eight such habitat-patches (Fig. 2) for further analysis. In upland stands: two patches are dominated by *Acer saccharum* (in areas of high soil pH and Ca), two ‘mixed upland’ patches (with well-developed hard-pan) support combinations of *Fagus*, *Tsuga*, and *Acer* spp; and two patches are *Tsuga*-dominated (on soils of low pH, deep mor humus). Two patches of wet, peaty soils are dominated by *Picea* spp. and, especially, *Thuja*. One can also recognize two, less spatially coherent groups of ‘mixed swamp’ plots with mixed peaty and mineral soils, and mixed dominance of wetland and upland species; these are not generally treated as distinct habitat-patches. Plots in terminal groupings of cluster analyses may be assigned to disjunct patches of similar composition, but plots in a particular habitat-patch are always in the same terminal cluster. Some plots are not assigned to patches.

As reported in Woods (2000b) for upland habitats, shade-tolerant canopy species increased in abundance (both density and basal area; Fig. 3) for all habitat-patches (including *Thuja* in swamp forests not previously analysed), over the extended study period, and over most sub-intervals. However, *Fagus* increases from 1935 to 1990 were reversed after 1992, and effects of the 2002 storm are visible as basal area losses for both *Fagus* and *Acer* spp. Summary data for basal area by habitat-patch and measurement period are in App. 1.

Other species showed less consistent patterns across patches and habitat-types but trends were similar for patches of similar habitat (with the exception of *Acer rubrum*, where trends are inconsistent at all scales). Persistent and accelerating declines in *Betula* basal area are evident in most upland patches, but *Betula* increased in peatland patches. Less abundant species were either subcanopy species (*Ostrya virginiana* and *Abies bals-*

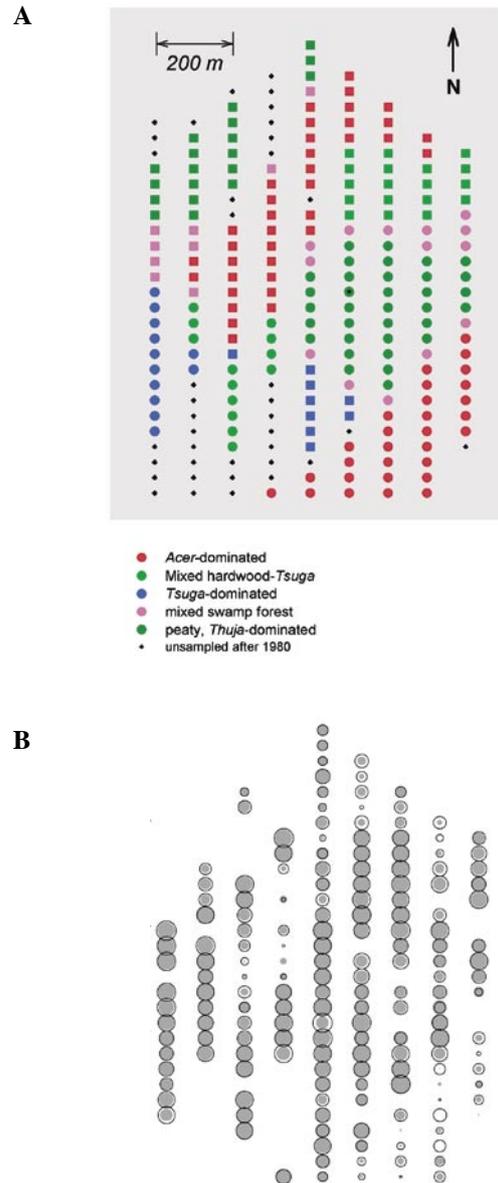


Fig. 2. Stand map showing (A) habitat-patches and (B) changes in plot diversity. **A.** Color indicates dominance (see legend), different symbols indicated coherent patches; color-symbol combinations are used similarly in Fig. 3. *Acer*-dominated patches have high soil pH and Ca; *Tsuga*-dominated patches low pH, deep mor; mixed hardwood patches shallow hard-pan (compare to Woods 2000b); mixed swamp forests discontinuous peat-mineral soil; *Thuja*-dominated patches deep peats. **B.** Areas of superimposed circles are scaled to initial and ending diversity (Shannon’s *H*) for each plot. Open, outlined circles show diversity in 1935; gray, unbordered circles are scaled to *H* values for 1999-2001 (pre-storm) (only plots sampled in both periods shown). Light-edged ‘bull’s-eyes’ (for example, in *Acer*-dominated areas) indicate decreasing diversity over time. Other diversity and equitability indices show similar patterns.

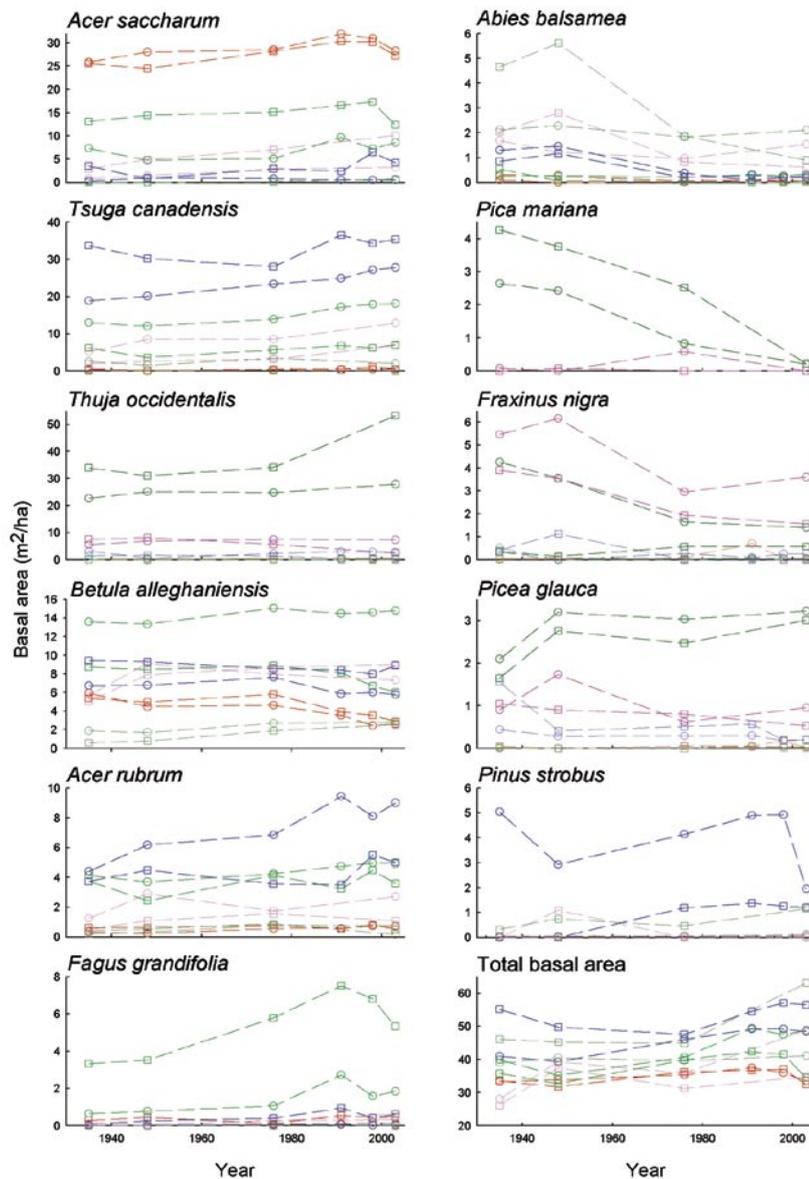


Fig. 3. Patch-scale species dynamics: Symbols and colors as in Fig. 2. Upland patches show six measurement periods, swamp-forest patches, four. All species with sustained basal areas $> 1 \text{ m}^2/\text{ha}$ are shown. (See App. 1 for full statistics by habitat-patch, Woods 2000 for more detailed demographic data for dominant upland species.)

mea, although the latter may be a canopy tree in peatland stands) or less-tolerant canopy trees, and, in most patches, declined in basal area. *Abies balsamea*, *Picea mariana*, and *Ostrya virginiana*, all largely restricted to particular habitats, declined by 50% or more from 1935 to modern measurements.

Predictability. Coherence of trajectories in ordination space varied with habitat-type and among measurement intervals. For most sample intervals, MRPP comparisons of plot change vectors did not distinguish between patches of similar composition and habitat ($p < 0.05$ only for comparison between ‘mixed upland’ patches for intervals including the 2002 storm). When similar patches are pooled (*Acer*-dominated, mixed, *Fagus*-dominated,

swamp-conifer), all pair-wise comparisons between habitat-types were significant for all measurement intervals ($p < 0.01$). Over sequential measurement intervals (prior to the 2002 storm), coherence appeared to increase over time in *Acer*-dominated patches (vectors in ordination space, Fig. 4; MRPP for comparison between sample intervals, $p = 0.06$), but *Tsuga* patches may show the reverse pattern, with more chaotic patterns for recent decades (Fig. 4; MRPP, $p = 0.09$). In upland habitat-types, pre-storm to post-storm vectors were generally less coherent than for other intervals. Coherence of trajectories was generally lower for swamp-forest plots (Fig 4).

‘Composition predictability’ showed predicted declines with increasing elapsed time (Mantel test results: Fig. 5). R -values are generally lower for ‘trajectory pre-

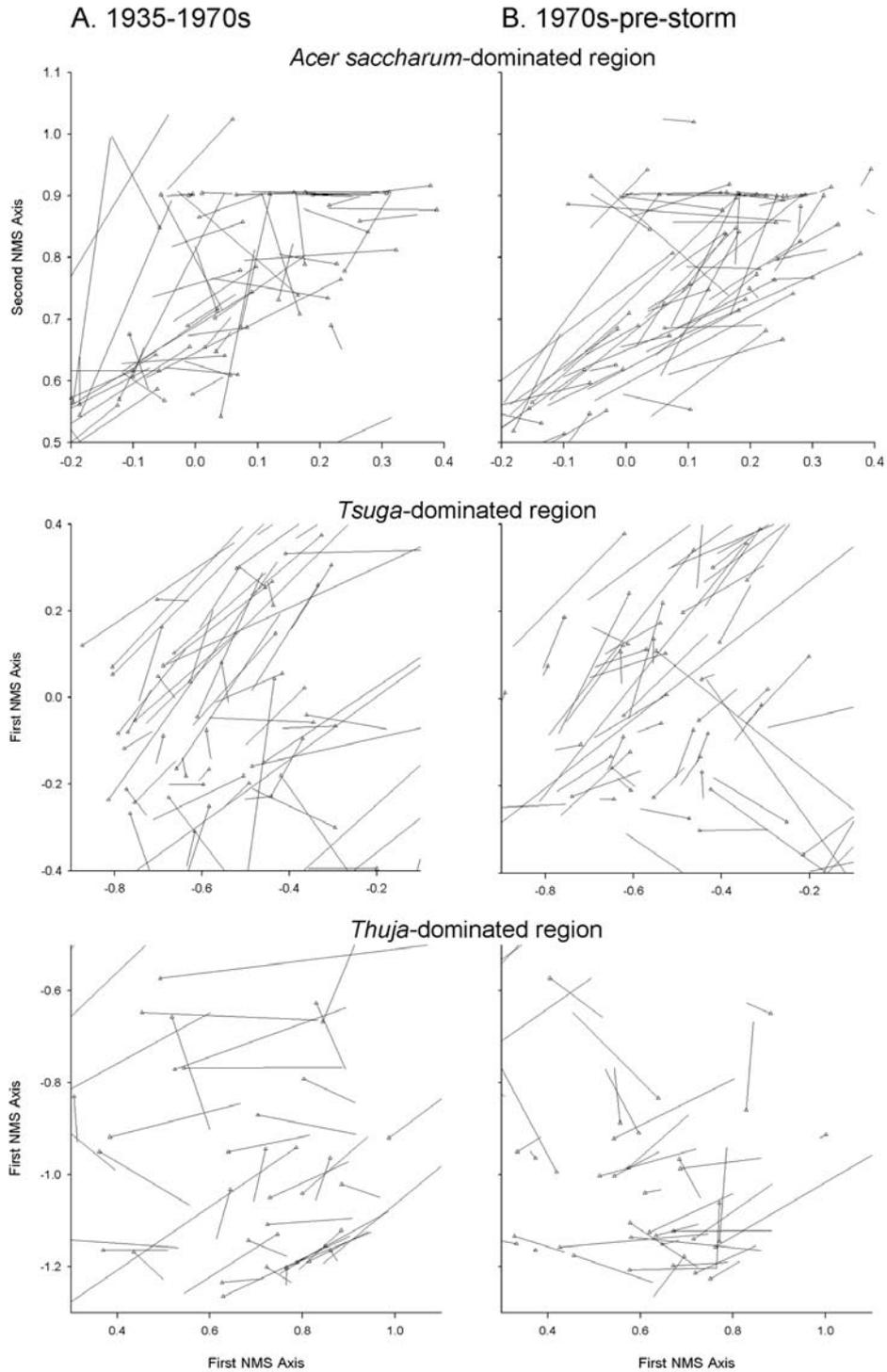


Fig. 4. Portions of plot trajectories in selected areas of ordination space. Vectors are for (A) 1935 to 1970s (ca. 40 year) and (B) 1970s to pre-storm (ca. 25 year) in a multi-temporal NMS ordination (all trajectories extracted from a single ordination of all measurements of all plots). Triangles are most recent end of vector. Panels show regions of ordination dominated by *Acer saccharum* (top row), *Tsuga canadensis* (middle) and *Thuja occidentalis* (bottom). Relative coherence of trajectories (predictability) varies with both time interval and position in compositional space.

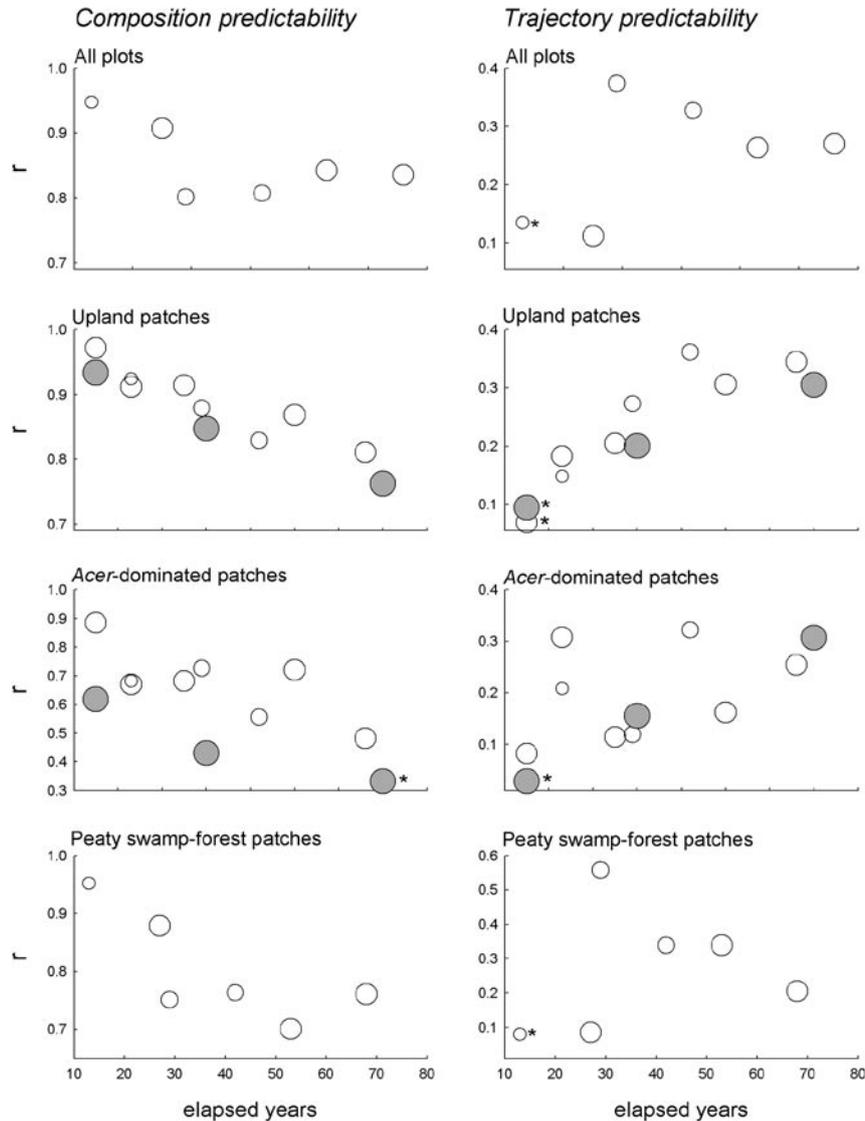


Fig. 5. Mantel test results: Mantel results, graphed as Pearson coefficient, r , for different sampling intervals & subsets of sample plots, as a function of elapsed time. ‘Composition predictability’ (left column) reflects correspondence between starting and ending composition; ‘trajectory predictability’ (right column) corresponds between starting composition and change vectors. Size of symbol is scaled to ending year of sampling interval; larger symbols indicate periods ending more recently. Shaded symbols represent periods ending in 2002–2004, after the 2002 blow-down. All r -values have associated probabilities < 0.01 except those indicated by asterisks. Patch types correspond to those identified in Fig. 2.

dictability’ (Fig. 5) but, also as expected, increase with elapsed time. While probabilities associated with Mantel statistics were < 0.01 for most tests (Fig. 5), these values should be treated cautiously (see Methods). Results for mixed upland and hemlock patches (not shown in Fig. 5) displayed qualitatively similar patterns. For upland (particularly *Acer*-dominated) patches, the 2002 blow-down decreased composition predictability; intervals ending with the post-storm sample were associated with lower r -values than other intervals of similar length (Fig. 5). The event’s effect on trajectory predictability is not distinguishable.

Predictability is lower for wetland patches and trends with time-interval less well-defined, perhaps because sampling intervals are less varied. Sample size effects

may be important; many outlying points (Fig. 5) involve the 1948 sample, with plot numbers half those for other periods.

Convergence and diversity. The distribution of plot-plot distances for all plots changed from 1935 to the pre-storm measurement (Fig. 6: Kolmogorov-Smirnov test, $p < 0.001$). Overall, the distribution increased in breadth and in median value. However, frequencies of both small and great distances increased, suggesting that, while similar plots became more similar (convergence), already dissimilar plots became more dissimilar (divergence). This combination of local (in species-space) convergence and global divergence, tending towards bimodality of distance distributions, is as predicted for

successional convergence towards different compositions under different habitat conditions. The 1974-1980 distribution (not shown) was intermediate and different from both 1935 or pre-storm distributions ($p < 0.05$). Upland plots, treated separately, show the same pattern in more pronounced form, while no change is detectable in distributions for swamp-forest plots. Within particular upland habitat-types modal distances decreased, and distribution changes were significant ($p < 0.05$), due primarily to increases in small plot-plot distances; frequencies of larger distances declined, suggesting convergence towards a single compositional ‘attractor’ for each habitat-type. For upland plots, the post-storm distribution was intermediate between 1935 and pre-storm distributions, and different from each ($p < 0.05$); small distances, in particular, were less frequent after the storm.

Plot-level diversity (both H and J) declined overall from 1935 to the pre-storm sample interval (Fig. 2B; single-factor, repeated-measures ANOVA with plots as subjects, $n = 176, p < 0.001$ for $H, p < 0.05$ for J); separate analyses for the 1935 to 1970s interval and the 1970s to pre-storm interval showed significant changes only for the 1970s to pre-storm interval. Repeated-measures ANOVAs with plots nested within habitat-patches (eight patches; ‘mixed swamp’ plots were excluded because they did not constitute well-defined spatial patches) showed a significant patch effect ($n = 154, p < 0.01$). When subsets of plots from patches of similar habitat-type were subjected separately to ANOVA (e.g., plots from the two *Acer*-dominated patches only) no patch effect was evident, and analysis of the full data-set with nesting of plots into four habitat-types (two patches pooled for each type; see Fig. 2A, Table 1) showed a habitat-type effect similar to the patch effect in the analysis with all eight patches. Further comparisons address plots pooled by habitat-type. Diversity (H) decreased within the three upland habitat-types from 1935 to the recent measurement (t -test, $p < 0.05$), but not in *Thuja*-dominated swamp-forest patches (Table 1); decreases in evenness (J) were significant only

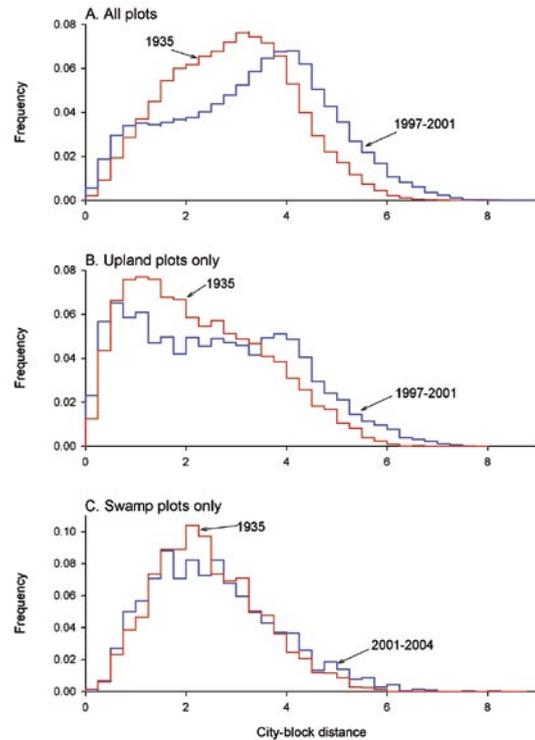


Fig. 6. Distributions of plot-plot distances in species-space: Histograms show frequencies of Sørensen distances between all pairs of plots in species-space for indicated sampling periods, for (A) all plots; (B) all plots in upland plot-groups (Fig. 2); (C) plots assigned to swamp forest plot-groups. In all graphs, blue curves represent the more recent sampling period.

for *Acer*-dominated patches. No comparisons showed significant differences between 1935 and 1970s sample periods; diversity changes were concentrated in the latter half of the study period.

Table 1. Shannon’s H and evenness (J) by habitat-type (two patches combined for each type).

	No. of plots		H 1935	J 1935	H 1970s	J 1970s	H recent	J recent
<i>Tsuga</i> -dominated patches (blue symbols, Fig. 2)	21	Mean	1.16	0.67	1.15	0.59	1.04*	0.67
		SD	0.32	0.11	0.28	0.13	0.26	0.15
Mixed hardwood - <i>Tsuga</i> (light green symbols)	29	Mean	1.28	0.77	1.26	0.70	1.18*	0.73
		SD	0.26	0.13	0.27	0.14	0.32	0.16
<i>Acer</i> -dominated patches (red symbols)	63	Mean	0.58	0.43	0.56	0.33	0.41*	0.32*
		Sd	0.40	0.26	0.44	0.21	0.40	0.25
<i>Thuja</i> -dominated peatlands (dark green symbols)	41	Mean	1.01	0.55	1.10	0.52	0.93	0.50
		SD	0.40	0.18	0.37	0.16	0.35	0.17

* average plot values within habitat-type (patches pooled by habitat-type) for recent measurement period differ from 1935 values (t -test, $p < 0.05$)

Discussion

Compositional trends and scale. Continuing increases in dominance of shade-tolerant canopy species, described by Woods (2000b) for upland forests but evident in swamp forests as well, constitute the primary trends in all habitat-types, implying continued importance of successional, competitive processes in old-growth stands. Competitive sorting among shade-tolerant species appears to be habitat-specific, however, such that particular community trends vary at the patch scale, depending on habitat-type. Patches appear to become more differentiated, and more internally uniform over time.

Less-tolerant canopy species generally decreased, but patterns vary among species and across habitat-types. For example, while *Thuja* dominance increased in swamp forests, decreasing diversity was not as pronounced as in upland stands, and some less-tolerant species (e.g., *Acer rubrum* and *Betula alleghaniensis*) maintained or increased basal areas while decreasing in upland stands. It is possible that competitive sorting is less intense in swampy patches; light regimes (unpubl. data) are more variable in these stands, with higher average light availability in the understory, possibly due to higher disturbance frequencies.

Disturbances such as the 2002 storm may counter patch differentiation; by favoring broadly distributed, less-tolerant species (Woods 2004) they may be a homogenizing force at the stand scale. Extensive early establishment of *Betula alleghaniensis* observed on new tip-up mounds in large gaps due to the storm (unpublished data) is consistent with this possibility.

Predictability and scale. For the stand as a whole, both composition predictability and trajectory predictability show trends predicted for a slowly changing, late-successional stand with competition-driven dynamics. With upland 'background' canopy mortality ca. 1%/year (Woods 2000a, 2004), large compositional changes require several decades, and composition predictability is highest for shorter intervals between measurements. Trajectory predictability (predictability of change vectors) shows the opposite trend, presumably because effects of demographic stochasticity, at plot-scale, are 'averaged out' only over periods of at least several decades. Relatively chaotic and coherent dynamics may coexist at different temporal scales.

Strong dependence of predictability on scale and habitat is also apparent (Fig. 5). For example, trajectories are less predictable for swamp forest patches than for upland patches, consistent with the possibility that more open canopy in these stands permits more stochasticity in regeneration. Among upland patch-types, lower predictability within *Acer*-dominated patches and less

pronounced trends over measurement intervals may be a consequence of greater initial uniformity.

Coherent trajectories among plots within and between patches of similar habitat-type, with distinct differences between habitat-types, are also consistent with habitat-dependence of competitive or disturbance dynamics. High within-habitat consistency differs from findings of McCune & Allen (1985) for western US old-growth forests; this could be due to differences in spatial scale (more local here) or in effective successional time elapsed (greater here). Changes in vector coherence for sequential intervals of similar length (Fig. 4) suggest influence of particular historical events. For example declines of *Pinus strobus* in *Tsuga*-dominated patches and *Betula* in mixed-upland patches accelerating in the latter half of the study period (Fig. 3) may reflect aging of specific, disturbance-initiated cohorts (Woods 2004). Disturbance frequencies and effects may, in turn, be influenced by patch properties if, for example, there are species differences among habitat-determined competitive dominants in vulnerability to disturbance (Canham et al. 2001; Woods 2004). Effects of disturbance depend on pattern and extent of disturbance (Turner et al. 1998), and these, too, may depend on species' properties. For example, mortality due to the 2002 storm varied among species (Woods 2004), and this may be reflected in reduced composition predictability, for intervals including 2002, for some habitat-types but not others (Fig. 5).

Coherent or predictable change could also be due to external drivers, such as climate change, interacting with species' properties. Trends in *Fagus* abundance at the Dukes RNA may be related to recent, climate-driven regional expansion (Woods & Davis 1989) of the species, but this possibility cannot be assessed from current data, nor can future climate-driven trends be easily predicted at patch or stand scale.

Convergence, diversity, and scale. Whether observed change is seen as convergent or divergent (Lepš & Rejmánek 1991; Smith & Huston 1989) depends on resolution relative to scale of habitat variation. Here, convergence within patches (scales of 10s to 100s of m) in upland habitats is consistent with competitive sorting, perhaps tending toward eventual monodominance as suggested by SORTIE models for similar forests (Pacala et al. 1996) and as observed in some tropical forests (Hart 1990). However, divergent trends are evident at stand-scale when habitat-patches of different types are pooled suggesting strong influence of environment on competitive dynamics. This is at least partially in contrast with suggestions by Frelich et al. (1993) and Davis et al. (1994), for another old-growth forest in northern Michigan, that distinct patches of *Tsuga* and *Acer* dominance may be largely historical artifacts, sustained by internal

feedbacks and unrelated to underlying environmental differences. In wetland patches, beyond general increases in *Thuja* dominance, strong convergence within patches is not evident. Persistence of less-tolerant species suggests inhibition of competitive sorting, perhaps due to a more vigorous disturbance regime.

Chase (2003) predicted strong convergence to habitat-specific equilibria when regional species pools are small, connectivity among habitat patches is high, and disturbance rates are high. Trends here conform to the first two predictions, but not the third. Upland habitat patches show stronger convergence, but no evidence of higher disturbance rates; in fact, unpublished data and observation suggest higher disturbance rates in swamp forests. Perhaps higher disturbance rates in very late succession counter convergent tendencies by providing establishment opportunities for competitively inferior species.

Successional convergence should reduce diversity, at least within habitat-patches. Consistent with this prediction, plot-level diversity and evenness declined in upland plots generally (most markedly in *Acer*-dominated patches), but not in wetland habitat-patches. Diversity differences among upland patch-types may be related to disturbance history; diversity loss was strongly concentrated in the second half of the study period, consistent with accelerating mortality of cohorts of less shade-tolerant species (Woods 2000b). Impact of the 2002 storm was generally greatest in mixed upland habitat-patches (Woods 2004); if this habitat-type is more vulnerable to wind-disturbance generally, such events may have the effect of promoting higher diversity in mixed-upland patches. Other studies of diversity changes in late succession are few. Taverna et al. (2005) observed decreasing diversity in the herb stratum of old-growth forests in southeastern U.S., and suggested environmental and land-use changes as causal factors, but the pattern could also be consistent with competitive sorting in late succession.

Conclusions

Long-term, permanent-plot studies with repeated measurements are critical for insight into behavior of otherwise recalcitrant 'slow' systems like old-growth forests. However, complex data-structures due to inherited design, irregularities in measurement, and archival failures, can challenge interpretation and rigorous hypothesis-testing. I have tried to develop and apply robust analytic approaches that, despite these constraints, permit powerful use of repeated measurements on permanent plots to address questions about direction and changes in rates of change, spatial and temporal scaling effects,

and consequences of environmental and compositional variation. Salient conclusions regarding initial questions include:

- This ancient forest, free of stand-initiating disturbance for centuries, exhibits apparently successional dynamics at patch and stand scales. Observed dynamics are not consistent with equilibrium models; instead, they suggest that dynamics are driven by habitat-specific competitive sorting, which is also inconsistent with competition-neutral models.

- Predictability of change trajectories and future composition from current composition varies with spatial and temporal scale and among patches of differing habitat and composition. Compositional predictability is highest for shorter elapsed time intervals, but vectors of change are more predictable for longer intervals.

- Dynamics can depend on specific stand history. Patterns of change in particular patches appear to reflect historical contingencies.

- Composition tends to converge among plots within patches and in similar habitats, but can be divergent at larger spatial scales as within-patch convergence produces between-patch differentiation. Convergence appears to be generally, but complexly associated with declining diversity.

These results emphasize the importance of addressing questions about community dynamics with observational data of appropriate scale and resolution. It remains to be seen whether complex data-sets of this sort can effectively be translated into predictive models. Powerful use of such data-sets calls for data-management and analysis tools that are robust with respect to irregularities in design and data structure.

Acknowledgments. This research was funded by the Andrew W. Mellon Foundation, the National Science Foundation, and the United States Forest Service. Over 25 Bennington College students participated in all aspects of the research. U.S. Forest Service staff provided support throughout the study. I particularly thank: Dr. Fred Metzger, who sustained the study and led remeasurements through the 1970s; Dr. Tom Crow and Jan Schultz, who facilitated use of data from pre-1980 measurements; and the rangers and staff of the Munising District of the Hiawatha National Forest. The paper has benefitted from comments and suggestions from three anonymous reviewers and by Dr. Helge Bruelheide.

References

- Abrams, M.D., Ruffner, C.M. & DeMeo, T.E. 1998. Dendroecology and species co-existence in an old-growth *Quercus-Acer-Tilia* talus slope forest in the central Appalachians, USA. *Forest Ecol. Manage.* 106: 9-18.
- Arseneault, D. & Sirois, L. 2004. The millennial dynamics of a boreal forest stand from buried trees. *J. Ecol.* 92: 490-504.
- Baker, P.J., Bunyavejchewin, S., Oliver, C.D. & Ashton, P.S. 2005. Disturbance history & historical stand dynamics of a seasonal tropical forest in western Thailand. *Ecol. Monogr.* 75: 317-343.
- Bakker, J.P., Olf, H., Willems, J.H. & Zobel, M. 1996. Why do we need permanent plots in the study of long-term vegetation dynamics? *J. Veg. Sci.* 7: 147-155.
- Bakker, J.P., Marrs, R.H. & Pakeman, R.J. 2002. Long-term vegetation dynamics: Successional patterns and processes. Introduction. *Appl. Veg. Sci.* 5: 2-6.
- Busing, R.T. & Mailly, D. 2004. Advances in spatial, individual-based modelling of forest dynamics. *J. Veg. Sci.* 15: 831-842.
- Canham, C.D., Papaik, M.J. & Latty, E.F. 2001. Interspecific variation in susceptibility to windthrow as a function of tree size and storm severity for northern temperate tree species. *Can. J. For. Res.* 31: 1-10.
- Chase, J.M. 2003. Community assembly: when should history matter? *Oecologia* 136: 489-498.
- Chesson, P.L. & Case, T.J. 1986. Overview: nonequilibrium community theories: chance, variability, history, and co-existence. In: Diamond, J. & Case, T.J. (eds.) *Community ecology*, pp. 229-239. Harper and Row, New York, NY, US.
- Christensen, N.L. & Peet, R.K. 1984. Convergence during secondary forest succession. *J. Ecol.* 72: 25-36.
- Davis M.B., Sugita S., Calcote R.R., Ferrari J.B. & Frelich L.E. 1994. Historical development of alternate communities in a hemlock-hardwood forest in northern Michigan, U.S.A. In: May, R., Webb, N. & Edwards, P. (eds.) *Large-scale ecology and conservation biology*, pp. 19-39. Blackwell, Oxford, UK.
- Franklin, J.F. & DeBell, D.S. 1988. Thirty-six years of tree population change in an old-growth *Pseudotsuga-Tsuga* forest. *Can. J. For. Res.* 5: 913-934.
- Frelich, L.E., Calcote, R.R., Davis, M.B. & Pastor, J. 1993. Patch formation & maintenance in an old-growth hemlock-hardwood forest. *Ecology* 74: 513-527.
- Fulton, M.R. & Harcombe, P.A. 2002. Fine-scale predictability of forest community dynamics. *Ecology* 83: 1204-1208.
- Gleason, H.A. & Cronquist, A. 1991. *Manual of vascular plants of northeastern United States and adjacent Canada*. New York Botanical Garden, New York, NY, US.
- Harcombe, P.A., Bill, C.J., Fulton, M., Glitzenstein, J.S., Marks, P.L. & Elsik, I.S. 2002. Stand dynamics over 18 years in a southern mixed hardwood forest, Texas, USA. *J. Ecol.* 90: 947-957.
- Hart, T.B. 1990. Monospecific dominance in tropical rain forests. *Trends Ecol. Evol.* 1: 6-11.
- Henry, J.D. & Swan, J.M.A. 1974. Reconstructing forest history from live and dead plant material – an approach to the study of forest succession in southwest New Hampshire. *Ecology* 55: 772-783.
- Hubbell, S.P. 2001. *The Unified neutral theory of biodiversity and biogeography*. Princeton University Press, Princeton, NJ, US.
- Lepš, J. & Rejmánek, M. 1991. Convergence or divergence: What should we expect from vegetation succession? *Oikos* 62: 261-264.
- McCune, B. & Allen, T.F.H. 1985. Will similar forests develop on similar sites? *Can. J. Bot.* 63: 367-376.
- McCune, B. & Grace, J.B. 2002. *Analysis of ecological communities*. MjM Software Design, Gleneden Beach, OR, US.
- McCune, B. & Mefford, M.J. 1999. *PC-ORD. Multivariate Analysis of Ecological Data*. Version 4.36. MjM Software, Gleneden Beach, OR, US.
- Pacala, S.W., Canham, C.D. & Ribbens, E. 1996. Forest models defined by field measurements: Estimation, error analysis & dynamics. *Ecol. Monogr.* 66: 1-43.
- Parshall, T. 1995. Canopy mortality & stand-scale change in a northern hemlock-hardwood forest. *Can. J. For. Res.* 25: 1466-1478.
- Pickett, S.T.A. 1989. Space for time substitution as an alternative to long-term studies. In: Likens, G.E. (ed.) *Long-term studies in ecology*, pp. 110-135. Springer, New York, NY, US.
- Smith, T. & Huston, M. 1989. A theory of the spatial & temporal dynamics of plant communities. *Vegetatio* 83: 49-69.
- Taverna, K., Peet, R.K. & Phillips, L.C. 2005. Long-term change in ground-layer vegetation of deciduous forests of the North Carolina Piedmont, USA. *J. Ecol.* 93: 202-213.
- Turner, M.G., Baker, W.L. & Peterson, C.J. 1998. Factors Influencing Succession: Lessons from Large, Infrequent Natural Disturbances. *Ecosystems* 1: 511-523.
- Woods, K.D. 2000a. Dynamics in late-successional hemlock-hardwood forests over three decades. *Ecology* 81: 110-126.
- Woods, K.D. 2000b. Long-term change & spatial pattern in a late-successional hemlock-northern hardwood forest. *J. Ecol.* 88: 267-282.
- Woods, K.D. 2004. Intermediate disturbance in a late-successional hemlock-northern hardwood forest. *J. Ecol.* 92: 464-476.
- Woods, K.D. & Davis, M.B. 1989. Paleocology of range limits: Beech in the Upper Peninsula of Michigan. *Ecology* 70: 681-696.

Received 8 February 2006;

Accepted 2 March 2006;

Co-ordinating Editor: H. Bruelheide.

*For App. 1, see also JVS/AVS Electronic Archives;
www.opuluspress.se/*